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How Many Ferns Are There in One Hectare of Tropical Rain Forest?

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The number of species of ferns in the Neotropics can be estimated to be about 3500. Pteridophytes have been treated in several recent neotropical floras (e.g., Lellinger, 1989; Proctor, 1985; Tryon and Stolze, 1989a, 1989b, 1991, 1992, 1993, 1994) and the fern flora has been documented for a number of local areas, for example La Selva (McDade et al., 1994), Barro Colorado (Croat, 1978), Rio Palenque (Dodson and Gentry, 1978), or Rio Abiseo N.P. (Young and León, 1991), but very few attempts have been made to make total pteridophyte species counts on a small-scale or to include quantitative measurements.

In a total species count in 0.01 ha of rain forest in Costa Rica, Whitmore et al. (1985) found 21 species and 204 individuals of ferns, including free-standing plants (9 species, 107 individuals), climbers (3, 10) and epiphytes (9, 87). In Peru, Young and León (1989) sampled approximately two hectares (10 m × 2 km) and found 61 species of ferns and fern allies on the ground; Tuomisto and Ruokolainen (1994) collected ferns up to 2 m above the ground in two transect plots of 0.35 ha and found 35 and 36 species, in each plot respectively, but there was no attempt to include all of the epiphytic species.

The present investigation is to our knowledge the first documentation of the total number of species of ferns and fern allies in a one hectare plot in a tropical lowland rain forest.

STUDY AREA AND METHODS

The study site was located at ca. 250 m elevation in the Reserva de Producción Faunística Cuyabeno, in Amazonian Ecuador (00°00′S, 76°12′W). Annual precipitation at Tarapoa, about 12 km from the site, is 3555 mm. A square hectare plot was established in non-flooded rain forest vegetation (terra firme) avoiding major recent tree fall gaps. Topographical relief in the landscape of the area was minor and the difference between the highest and lowest points of the plot was ca. 20 m (Fig. 1A). The soil was clayey and varied in color from gray-brown in the lower parts to orange-red in the upper part of the plot. The sample plot had trees up to ca. 40 m in height, but only 12 trees were taller than 30 m (Valencia and Balslev, unpublished data) and the species richness of trees larger than 5 cm as well as 10 cm diameter at breast height is presently the world's record (Valencia and Balslev, 1994). The plot also contains a substantial number of small trees and shrubs (Christensen and Balslev,

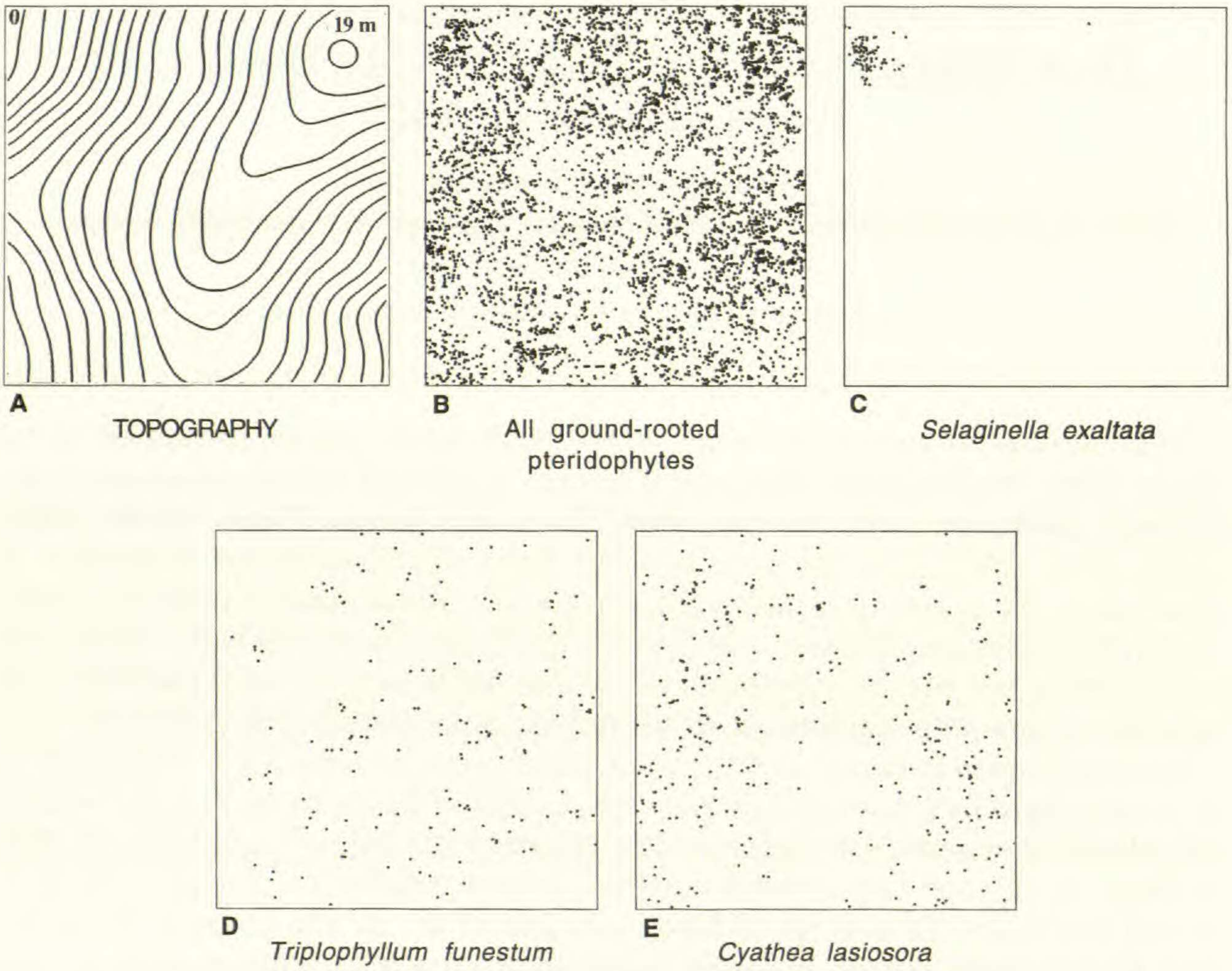

FIG. 1. Topography (A), distribution of all ground pteridophytes (B), and examples of edaphic-topographic specialization (C–E): *Selaginella exaltata* in the wettest area of the plot approaching a swamp (C); *Cyathea lasiosora*, a slope species (D); *Triplophyllum funestum*, which is less abundant in wet areas and on lower slopes (E).

unpublished data), 100 species of lianas (Paz y Miño et al., unpublished data), and 71 species of herbaceous angiosperms in the ground layer (Poulsen and Balslev, 1991).

Ground ferns include terrestrials, scandents, juvenile climbers, and fallen and established epiphytes and climbers. Terrestrials are rooted in the ground and complete their life cycles without support from other plants. Scandents always germinate on the ground and depend to some extent upon leaning on other plants. Climbers may germinate on the ground and are, as are epiphytes, closely adhered to the supporter, and depend in most cases on this connection to produce spores.

In April–June 1988, every individual of rooted ground fern in the plot was identified and mapped, cover was estimated, and heights of individuals of the tree fern *Cyathea lasiosora* (=*Trichipteris nigra* (C. Martius) R.M. Tryon) were measured by the first author. Cover was estimated as the vertical projection of the leaf area on a horizontal plane. In the same period, epiphytic species (including climbers) in the plot were studied by the second author on more than half of the trees larger than 10 cm diameter at breast height (dbh). Because the trees had to be climbed using tree grippers, only epiphytes growing close enough to the tree trunk to be reached by this method could be sampled. Consequently, quantitative estimates of fern abundance could not be obtained for the whole volume of the canopy. Also, if there are species that grow exclusively in the outer parts of the canopy of a tree, these may not have been recorded at all.

Voucher material from each study was compared in order to ensure that identifications were correlated. Vouchers are at QCA and AAU.

Results

Fifty species of pteridophytes were documented in the 1 ha plot (Table 1). Half of these species were rooted in the ground, comprising 16 terrestrial species (32%), 3 scandent species (6%), and 6 species of climbers (12%); the other half were epiphytes. The terrestrials included the single tree fern species encountered in the plot, *Cyathea lasiosora.* The numbers of ground fern species in subplots of 10 m × 10 m within the plot ranged from 4 to 14, with an average of 8.3 (n = 100), and the number of terrestrial species (including *C. lasiosora*) in the subplots varied between 2 and 8 (average 4.6).

Two of the species with a general climbing life form only occurred on the ground in low numbers (*Cyclodium meniscioides* and *Polybotrya caudata*) and were not collected above the ground layer at all. These climbers are examples of rare species, and they may never ascend into the canopy.

Forty-nine individuals of species that in general have an epiphytic life form were found on the forest floor, in most cases because they had fallen down from the trees. Ten of these individuals from three species (*Asplenium cirrhatum, Elaphoglossum styriacum,* and *Nephrolepis rivularis*) were rooted, and it is possible that they germinated there; the remaining 39 were not established and had undoubtedly fallen.

On the forest floor, 4637 rooted individuals were recorded. Within the plot, the number of rooted individuals in 10 m × 10 m subplots ranged from 11-89 (average 46.4, n = 100). Juvenile climbers constituted 32% of the ground pteridophytes. Total cover of all pteridophytes at ground level was estimated to be 85 m^2. The terrestrial species accounted for 68.3 m^2 cover, 28.8 of which was due to the tree fern. Scandents accounted for 5.5 m^2, climbers at ground level for 11.2 m^2, and established epiphytes on the forest floor were insignificant (0.05 m^2).

The total density of all ground-rooted pteridophytes was distributed over the plot in an apparently random way (Fig. 1B). However, the distribution patterns of the individual species often were clearly non-random and showed a distinct dependence on topography. For example, *Selaginella exaltata* was much more abundant in the lowermost part of the plot where the ground may be covered by water for short periods after heavy rain (Fig. 1C); *Triplophyllum funestum* avoided the lowermost parts, being more common on the central ridge of the plot (Fig. 1 D). The tree fern *Cyathea lasiosora* was most abundant

TABLE 1. List of the pteridophyte species recorded within a 1-ha plot of terra firme forest at Cuyabeno, Amazonian Ecuador. A voucher number is given in parentheses. Observed life forms of the species are given as terrestrial (T), scandent (S), climber (C) or epiphyte (E). The number of individuals at ground level rooted in the ground is given in brackets.

Adiantum humile Kunze (*Poulsen 78617*); T [914]
Adiantum obliquum Willd. (*Poulsen 80987*); T [1]
Adiantum terminatum Kunze (*Poulsen 78362*); T [1004]
Anetium citrifolium (L.) Splitgb. (*Nielsen 76484*); E
Antrophyum guayanense Hieron. (*Nielsen 76307*); E
Asplenium cirrhatum Willd. (*Nielsen 76430*); E, Occasionally T [4]
Asplenium cuneatum Lam. (*Nielsen 76421*); E
Asplenium juglandifolium Lam. (*Nielsen 76337*); E
Asplenium serratum L. (*Nielsen 76308*); E
Campyloneurum ophiocaulon (Klotzsch) Fée (*Nielsen 76470*); E
Cyathea lasiosora (Kuhn) Domin (*Poulsen 78531*); T [317]
Cyclodium meniscioides (Kunze) Mett. (*Poulsen 80147*); C [16]
Danaea cf. *ulei* H. Christ. (*Poulsen 80222*); T [22]
Danaea leprieurii Kunze (*Poulsen 80977*); T [5]
Dicranoglossum desvauxii (Klotzsch) Proctor (*Nielsen 76457*); E
Elaphoglossum laminarioides (Fée) T. Moore (*Nielsen 76242*); E
Elaphoglossum luridum (Fée) H. Christ (*Nielsen 76454*); E
Elaphoglossum styriacum Mickel (*Poulsen 78935*); E, Occasionally T [1]
Elaphoglossum tenuiculum (Fée) Baker (*Poulsen 80504*); E
Hymenophyllum polyanthos (Sw.) Sw. (*Nielsen 76357*); E
Lindsaea divaricata Klotzsch (*Poulsen 79558*); T [41]
Lindsaea lancea (L.) Bedd. var *lancea* (*Poulsen 79166*); T [1]
Lindsaea sp. (*Poulsen 78942*); T [1]
Lomagramma guianensis (Aubl.) Ching (*Nielsen 76145*); C [321]
Lomariopsis nigropaleata Holttum (*Nielsen 76440*); C [177]
Microgramma baldwinii Brade (*Nielsen 76500*); E
Microgramma fuscopunctata (Hook.) Vareschi (*Nielsen 76466*); E
Microgramma megalophylla (Desv.) Sota (*Nielsen 76124*); E
Microgramma reptans (Cav.) A.R. Sm. (*Nielsen 76228*); E
Nephrolepis rivularis (Vahl) Krug (*Nielsen 76349*); E, Occasionally T [5]
Pecluma cf. *ptilodon* (Kunze) M.G. Price (*Nielsen 76462*); E
Polybotrya caudata Kunze (*Poulsen 80506*); C [2]
Polybotrya osmundacea Willd. (*Nielsen 76412*); C [269]
Polybotrya pubens Mart. (*Nielsen 76158*); C [690]
Polypodium bombycinum Maxon (*Nielsen 76380*); E
Polypodium richardii Klotzsch (*Nielsen 76324*); E
Polypodium triseriale Sw. (*Poulsen 80960*); E
Saccoloma inaequale (Kunze) Mett. (*Poulsen 78382*); T [170]
Salpichlaena hookeriana (Kuntze) Alston (*Poulsen 79986*); S [27]
Salpichlaena volubilis (Kaulf.) J. Sm. (*Poulsen 80602*); S [84]
Selaginella exaltata (Kunze) Spring (*Poulsen 80975*); S [72]
Selaginella parkeri (Hook. & Grev.) Spring (*Poulsen 80954*); T [8]
Selaginella revoluta Baker (*Poulsen 80484*); T [1]
Thelypteris biformata (Rosenst.) R.M. Tryon (*Poulsen 79978*); T [4]
Trichomanes ankersii Hook. & Grev. (*Nielsen 76282*); E
Trichomanes pinnatum Hedw. (*Poulsen 80562*); T [317]
Trichomanes punctatum Poir. ssp. *sphenoides* (Kunze) Wess. Boer (*Nielsen 76353*); E
Triplophyllum dicksonioides (Fée) Holttum (*Poulsen 80325*); T [2]
Triplophyllum funestum (Kunze) Holttum (*Poulsen 78209*); T [161]
Vittaria lineata (L.) Sm. (*Nielsen 76203*); E

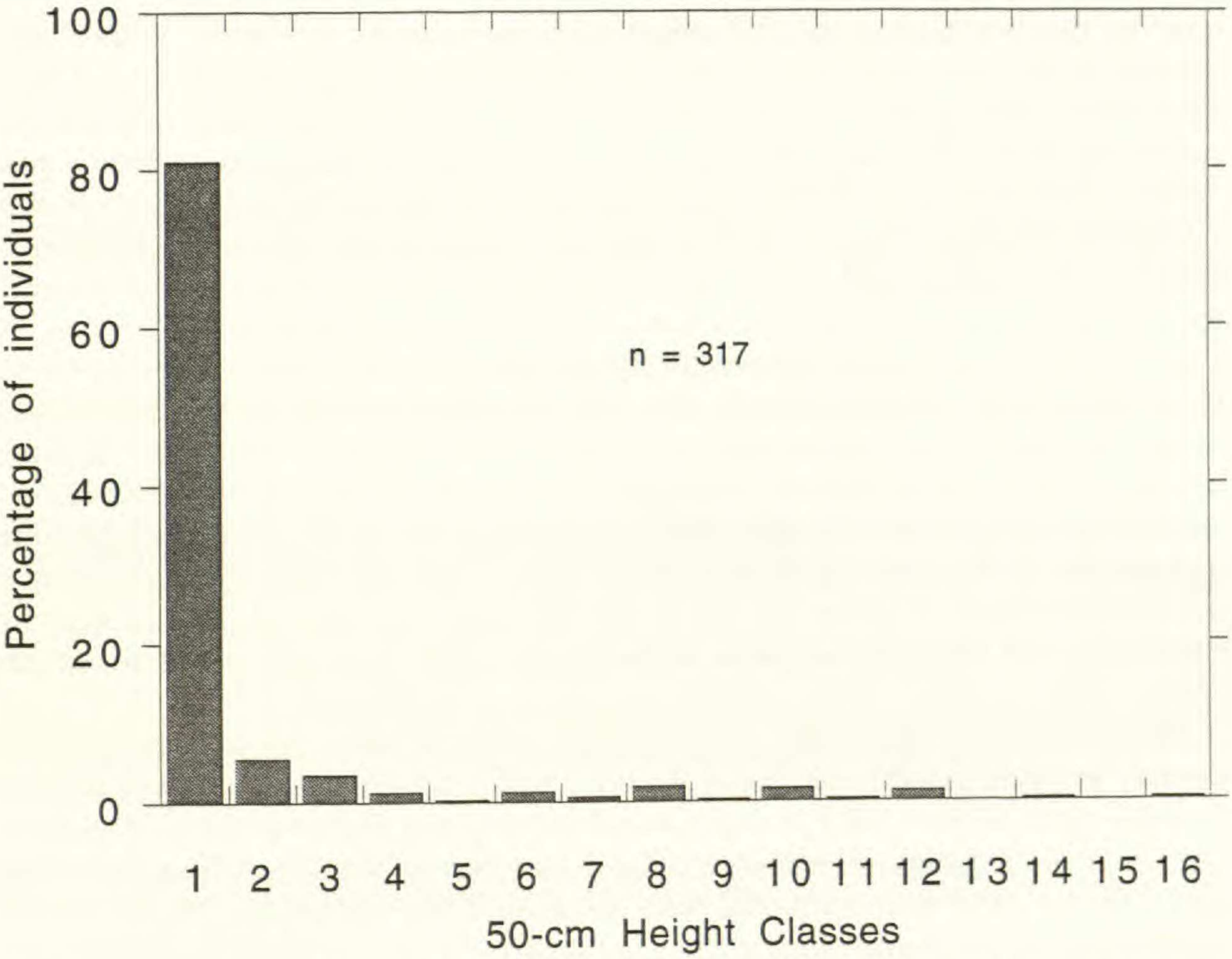

FIG. 2. Distribution in the 1 ha plot of individuals in various height classes of *Cyathea lasiosora*.

on the slopes in the plot (Fig. 1E), and most of the individuals (82%) were shorter than 0.5 m (Fig. 2); four of the larger individuals were fertile. The tallest individuals of *C. lasiosora* were found in the lowest part of the plot.

Some species occurred in such low abundance that it was not possible to state anything with certainty about their distribution patterns. *Nephrolepis rivularis* is one such example, but the five individuals of this species were all found on the ground in a small gap, with additional individuals on fallen branches.

DISCUSSION

The average number of ground ferns per 0.01 ha in Cuyabeno, as well as the proportion of epiphytic species of all ferns, is comparable to results from a 0.01 ha plot in Costa Rica (Whitmore et al. 1985). The density of ground ferns (free-standing plants) in that study is, however, higher than the maximum density and more than double the average of the 0.01 ha subplots in the Cuyabeno study. The high density recorded in the Costa Rican study may be explained by the fact that the plot was established in a building-phase forest (Whitmore et al. 1985) presumably with higher light intensities on the forest floor.

In the present study, the ground fern individuals are an important component of the herbaceous ground vegetation, accounting for 39% of the total density in the plot and 22% of the total ground herb cover (Poulsen and Balslev, 1991). This percentage was obtained excluding the tree fern individuals.

Ground ferns also were studied in a rain forest of the same altitude and annual precipitation in Borneo applying the same sampling techniques in two 1 ha plots (Poulsen, in press a). In a plot on a steep slope, where the difference between the highest and lowest points was about 60 m, 21 species of ground ferns were registered (1387 individuals, 21.6 m^2 cover). In a less steep plot at a dry ridge plateau (30 m difference) 15 species of ground ferns were registered (612 individuals, 10.1 m^2 cover). Whereas the distributions of all individuals of ground ferns were apparently random in the Cuyabeno plot, the density increased down-slope in both Bornean plots (Poulsen, in press b). This difference in overall pattern of ground ferns is probably due to the very steep general topography in that area of Borneo and a more monsoon-like climate with dry periods (Poulsen, in press b). As in the Bornean studies, several species in Cuyabeno had different edaphic preferences, a fact that will result in an increase in the number of co-existing species in a small area.

The structure of the forest is within the range of other neotropical forests, but can be considered to be low-statured when comparing to analogous forests in other parts of the world (Valencia and Balslev, unpublished data). The low-stature of the vegetation enhances light intensities on the forest floor, and this may explain why pteridophytes that in general are epiphytic can be found established on the forest floor in the Cuyabeno plot, but are not at all so in the Bornean plots (Poulsen, in press a).

The large number of juveniles of *Cyathea lasiosora* has also been documented in Peru by Young and León (1989), which they ascribed to either high mortality or growth suppression. The greater abundance of the largest individuals in the lowest part of our plot suggests that topographic/edaphic conditions (e.g., soil moisture) are important in the long term survival of individuals of this species.

The 50 species of pteridophytes is a minimum total, because we were not able to make a thorough investigation of the canopy. We do not, however, expect the actual species richness in the plot to be much larger. The total number of pteridophyte individuals in the plot is probably much larger than the value found for ground ferns. The actual number of species of pteridophytes will probably be less than 5% of the total number of vascular plant species in the 1 ha plot. This estimate is reached combining references for the other life forms in the plot (Poulsen and Balslev, 1991; Christensen and Balslev, unpublished data; Valencia and Balslev, 1994; Paz y Miño et al., unpublished data).

The present investigation provides a snapshot of the ferns in a small area in Amazonian Ecuador. When similar data become available from other sites in South America and are combined with information on edaphic and climatic factors, it will be possible to make more general conclusions on patterns of species richness of ferns.

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LITERATURE CITED

CROAT, T. B. 1978. *Flora of Barro Colorado Island.* Standford University Press, Stanford, CA.

DODSON, C. H. and A. H. GENTRY. 1978. Flora of the Río Palenque Science Center, Los Ríos, Ecuador. Selbyana 4:1-628.

LELLINGER, D. B. 1989. The ferns and fern allies of Costa Rica, Panama, and the Chocó (part 1: Psilotaceae through Dicksoniaceae). Pteridologia 2A:1–364.

MCDADE, L. A., K. S. BAWA, H. A. HESPENHEIDE, and G. S. HARTSHORN, EDS. 1994. *La Selva. Ecology and natural history of a neotropical rainforest.* University of Chicago Press, Chicago, IL.

POULSEN, A. D. and H. BALSLEV. 1991. Abundance and cover of ground herbs in an Amazonian rain forest. J. Veg. Sc. 2:315–322.

POULSEN, A. D. In press a. The herbaceous ground flora of the Batu Apoi Forest Reserve, Brunei. Proceedings of the conference: Tropical Rain Forest Research—Current Issues.

POULSEN, A. D. In press b. Species richness and density of ground herbs within a plot of lowland rain forest in NW Borneo. J. Trop. Ecol.

PROCTOR, G. R. 1985. *Ferns of Jamaica.* British Museum (Natural History), London.

TRYON, R. M. and R. G. STOLZE. 1989a. Pteridophyta of Peru. Part I. 1. Ophioglossaceae–12. Cyatheaceae. Fieldiana Bot., n.s. 20:1-145.

———. 1989b. Pteridophyta of Peru. Part II. 13. Pteridaceae–15. Dennstaedtiaceae. Fieldiana Bot., n.s. 22:1-128.

———. 1991. Pteridophyta of Peru. Part IV. 17. Dryopteridaceae. Fieldiana Bot., n.s. 27:1-176.

———. 1992. Pteridophyta of Peru. Part III. 16. Thelypteridaceae. Fieldiana Bot., n.s. 29:1-80.

———. 1993. Pteridophyta of Peru. Part V. 18. Aspleniaceae–21. Polypodiaceae. Fieldiana Bot., n.s. 32:1-190.

———. 1994. Pteridophyta of Peru. Part VI. 22. Marsileaceae-28. Isoetaceae. Fieldiana Bot., n.s. 34:1-123.

TUOMISTO, H. and K. RUOKOLAINEN. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. J. Veg. Sci. 5:25–34.

VALENCIA, R and H. BALSLEV. 1994. High alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation 3:21–28.

WHITMORE, T. C., R. PERALTA, and K. BROWN 1985. Total species count in a Costa Rican rain forest. J. Trop. Ecol. 1:375–378.

YOUNG, K. R. and B. LEÓN. 1989. Pteridophyte species diversity in the central Peruvian Amazon: Importance of edaphic specialization. Brittonia 41:388–395.

YOUNG, K. R. and B. LEÓN. 1991. Diversity, ecology and distribution of high-elevation pteridophytes within Abiseo National Park, north-central Peru. Fern Gaz. 14:25–39.